

Phenology of development and population characteristics of the small spruce bark beetle *Ips amitinus* (Eichh.) in the Karkonoski National Park

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ABSTRACT

In the years 2005–2006, in the Karkonoski National Park there were conducted observations on infestation of spruce trees by bark beetles (Col., Curculionidae, Scolytinae). Data on bark beetle species composition and frequency of occurrence of individual species were collected. The data on development phenology of the small spruce bark beetle *Ips amitinus* in the upper subalpine spruce forest sites (1000–1250 m a.s.l.) indicated higher frequency of occurrence of this species (26.3%) when compared to the European spruce bark beetle *Ips typographus*. The study included analyses of population size, density, fecundity and mortality of *I. amitinus*. The rate of development in *I. amitinus* in the Karkonosze Mts. is similar to that observed in the Alps. The number of laid eggs observed was low and the reproduction success was very high at minimal mortality. Establishment of feeding galleries and egg laying lasted several weeks and 1/3 of feeding galleries were found in the second series of trap trees.

KEY WORDS

Ips amitinus, development phenology, population traits, Karkonoski National Park

INTRODUCTION

The small spruce bark beetle *Ips amitinus* (Eichhoff 1872) is a species closely related to the European spruce (eight-toothed) bark beetle *Ips typographus* (Linnaeus 1758) and resembles the latter morphologically and biologically. Both species frequently co-habit same areas in tree stands or on dying trees together with other spruce bark beetle species. In the ecological sense these form a community of cambiophagous insects competing for environmental resources.

While there is available abundant information on *I. typographus*, one of the most important bark beetle species causing considerable economic losses, data on the small spruce bark beetle are not systematically presented. *I. amitinus* is described most frequently as a species accompanying *I. typographus* (Grodzki 1997, 2009). Only scarce studies have been devoted solely to the small spruce bark beetle (Annala and Nuorteva 1977; Stauffer and Zuber 1998; Jurec and Bojović 2004; Økland and Skarpaas 2008; Witrylak 2008; Holuša et al. 2012; Kicińska et al. 2012).

The small spruce bark beetle is found mainly in central Europe, including mountainous and alpine regions. In western Europe it reaches Belgium, the Netherlands and France.. In the east it is found in Russia (including its northern provinces), while in the south it reaches lowland areas in former Yugoslavia, Italy and Greece. In the 20th century the small spruce bark beetle started to expand its range in a northerly direction. In the 1930's it appeared in Estonia, while in the early 1950's it was first reported in Finland (Koponen 1975; Annila and Nuorteva 1977; Biermann and Thalenhorst 1977; Grodzki 1998; Økland and Skarpaas 2008). In the mountainous regions, where *I. amitinus* is typically found more often than in the lowlands, it is observed up to the mountain forest limit and its highest reported range is altitude 2250 m a.s.l. (Nierhaus-Wunderwald and Forster 2004). This species was accidentally introduced with wood to the British Isles, Sweden, the USA and New Zealand (Lundberg 1995; Lindelöw 2000; Brockerhoff et al. 2006).

In Poland, the small spruce bark beetle is commonly found throughout the country, however to date it has not been reported in the Baltic coast, the Pomeranian Lake District and in the Świętokrzyskie Mts. (Burakowski et al. 1992).

Observations on the occurrence of spruce bark beetles in the mountain forest limit in the Karkonoski National Park conducted in the years 2001–2003 (Mazur et al. 2006; Mazur et al. 2008), showed a significant role and abundant occurrence of *I. amitinus* in bark beetle community colonizing upper alpine spruce forests in the Karkonosze Mts. The dominant role of the small spruce bark beetle was shown on stand edges in the case of stands with artificial spatial structure, aged approx. 70–140 years. In older stands, characteristic of spatial structure similar to natural, single spruces were infested by communities of bark beetles with a predominant share of *I. typographus*. The results of the above study indicated a need for further observations of tree infestation by bark beetles and it was attempted to explain the dominant role of the small spruce bark beetle (Mazur et al. 2006; Mazur et al. 2008).

In 2005 and 2006, in continuation of the aforesaid studies, further observations were conducted in the Karkonoski National Park (KNP) aiming at examination of:

- small spruce bark beetle biology and phenology of development,
- small spruce bark beetle population characteristics.

MATERIAL AND METHODS

Field observations were conducted in the Karkonoski National Park from the second half of May, 2005 to 8 September, 2005. In 2006, inspections were conducted on 5–7 June and 5–7 July.

For data collection there were used trap trees (series 1 and 2), produced from trees infested by bark beetles (description of the trees used in the analyses, including diameters and numbers of mother galleries is contained in Kuźmiński and Mazur, 2013). Observations on the trap trees were conducted in the western part of the park in the Szrenica, Śnieżne Kotły and Przełęcz protection zones. Inspections carried out in 2006 included the Śnieżka protection range. Bark beetle-infested trees were also identified in the upper subalpine coniferous forest zone throughout the park area, and these were not assigned as trap trees, but used for analyses of bark beetle population traits, i.e. the number of laid eggs, the length and number of mother galleries, as well as development success and mortality.

Observations were carried out on 22 trap trees (spruce long logs), 8 rollers 2.4 m long and 9 rollers 1.2 m long. On the logs and bolts there were marked 1-meter long sections and the diameters and numbers of feeding galleries were assessed for individual bark beetle species. In addition, mother galleries extending from the mating chamber were counted in selected long logs together with the number of established egg galleries and pupa cells at the ends of larval galleries. Most analyses were conducted after long logs and rollers had been debarked. Until the time of debarking a rate of feeding gallery development was examined by removing the bark from trees on the area of approx. 10 × 15 cm.

The method of data collection from trees follows recommendations on studying cambio- and xylophagous insects (Starzyk 1987).

Development phenology and population traits were also studied on bark beetle infested trees not used as conventional and unbarked traps (tab. 1).

Tab. 1. Phenology of development of small spruce bark beetle observed in 2005 and 2006 in the Karkonoski National Park

Date of control	Development stage
First half of May Cool period, typically in mid-May after a relatively sunny, but cool beginning of the month in 2005	No activity, lack of entrance holes
Second half of May Relatively cool and wet weather in 2005	Infestation and beginning of establishment of bark beetle mother galleries, reaching 3–4 cm in length Simultaneous emergence of numerous eight-toothed bark beetle and six-toothed spruce bark beetle
1–15 June	Further and more intensive establishment of mother galleries; gallery length: up to 7 cm; appearance of larval galleries of several mm in length
Second half of June First half of July	Development of larvae in galleries Larvae complete development by preparing pupa cells
Second half of July	Larvae still feed in feeding galleries, most of them turn into pupa stage and first light-coloured beetles are found. Young, discoloured beetles start secondary feeding under the bark On 2nd series trap trees, there is observed the beginning of feeding gallery establishment by the small spruce bark beetle; six-toothed spruce bark beetle predominates in tree crowns – also in establishing feeding galleries
Mid-August	Completion of development; some young beetles leave their galleries, other beetles remain in feeding galleries
First half of September	1 st series trap trees: beetles still remain in feeding galleries, some remain in feeding galleries for overwintering 2 nd series trap trees: mother galleries and well-developed larval galleries, no pupa cells

RESULTS

Small spruce bark beetle biology and phenology

In the course of observations on small spruce bark beetles there was found that the number of egg galleries in the mother gallery ranges from 9 to 48. Calculated on the basis of these data mean number of egg galleries per one mother gallery was 20.92.

Tab. 2. Percentage shares of small spruce bark beetle feeding galleries with different numbers of mother galleries extending from one mating chamber

Number of mother galleries	2	3	4	5	6	7
Share [%]	7.1	25.0	42.8	7.1	7.1	10.7

In single feeding galleries of small spruce bark beetles there extended 2–7 mother galleries from the mating chamber. For example, a total of 185 of small spruce bark beetle feeding galleries were recorded in one analyzed tree (no. 10, forest compartment 151a).

The proportions of feeding galleries with specific numbers of mother galleries are given in table 2. Development phenology of the small spruce bark beetle based on observations collected in the Karkonoski National Park is presented below (see also tab. 1).

Assessment of population parameters for *Ips typographus* and *Ips amitinus*

Population parameters were assessed mainly on the basis of data collected on spruces (standing and fallen) colonized by bark beetles and not used as trap trees. These trees were inventoried at altitudes of 750–1220 m a.s.l. (tab. 3).

Population size was typically limited to single trees or foci (bark beetle nests), and for *I. amitinus* it ranged from 0 to 185 feeding galleries per tree (on average 51), whereas for *I. typographus* – from 0 to 245 (on average = 35.32). The highest level was recorded on the half circumference of a felled spruce (from the Sowia Dolina area, diameter in the butt end = 70 cm, stem length = 26.3, 803 *I. typographus* feeding galleries).

Tab. 3. Results of survey on spruce infestation by European spruce bark beetle (*I. typographus*) and small spruce bark beetle (*I. amitinus*) in accordance with altitude in the Karkonoski National Park

Location [compartment]	Altitude	Species of bark beetle	Number of mother galleries	Number of exit holes	Control area [cm ²]
22b	1200	<i>Ips typographus</i>	13	—	22 × 54 = 1188
65d	1100		—	31	30 × 10 = 300
67g	1220		—	33	30 × 20 = 600
71i	1100		26	—	20 × 20 = 400
71i	1100		13	—	20 × 20 = 400
71k	1150		26	—	20 × 20 = 400
71k	1150		23	—	20 × 20 = 400
71r	1200		1	12	20 × 20 = 400
72j	1120		—	16	45 × 20 = 900
72j	1120		—	42	45 × 20 = 900
82c	1150		—	12	5 × 10 = 50
82c	1150		—	7	6 × 8 = 48
82c	1150		—	13	6 × 10 = 60
83f	1150		2	—	38 × 22 = 836
83f	1150		7	—	70 × 20 = 1400
83f	1150		—	15	36 × 20 = 720
155f	1200		5	6	15 × 10 = 150
155f	1200		8	14	15 × 10 = 150
155f	1200		9	9	15 × 10 = 150
155f	1200		12	—	30 × 50 = 1500
133j	750		4	—	30 × 44 = 1320
133j	750		13	—	30 × 44 = 1320
133j	750		3	—	9 × 5 = 45
163b	1100		7	37	25 × 15 = 375
72f	1150	<i>Ips amitinus</i>	14	—	40 × 20 = 800
72f	1150		13	—	40 × 20 = 800
72f	1150		13	—	40 × 20 = 800
71k	1150		13	—	20 × 20 = 400
71r	1200		7	—	20 × 20 = 400
72j	1120		—	22	45 × 20 = 900
72j	1120		—	53	45 × 20 = 900
73w	1150		—	6	40 × 10 = 400
73w	1150		—	27	20 × 40 = 800
139p	1030		24	—	10 × 50 = 500
139p	1030		21	—	35 × 17 = 595
163l	1200		11	—	10 × 10 = 100
163l	1200		8	9	10 × 10 = 100
194g	1000		32	—	25 × 100 = 2500

Population density for *I. amitinus* ranged from 1.75 to 11 galleries per 100 cm² – on average 2.16 galleries per 100 cm² (tab. 4). Depending on altitude the area covered by one mother gallery ranged from 23.1 to 52.8 cm². In other words, the greatest density of mother galleries burrowed by small spruce bark beetles was observed at approximate altitude 1200 m a.s.l., while it was the lowest in trees growing at altitudes from 1100 to 1199 m a.s.l. Also, the number of *I. amitinus* exit holes per unit area was higher in trees growing at altitude 1200 m than that observed in trees growing at lower altitudes (however, the latter conclusions are based on the limited number of observations).

Tab. 4. Mortality and reproduction success of European spruce bark beetle (*I. typographus*) and small spruce bark beetle (*I. amitinus*) at different altitudes in the Karkonoski National Park

Species of bark beetle	Altitude	Mother gallery/cm ²		Exit holes/cm ²	
		range	mean	range	mean
<i>Ips typographus</i>	750	15.0–330.0	134.2	–	–
	1100–1199	15.4–418.0	40.5	4.2–56.3	18.9
	1200–1220	16.7–400.0	73.7	10.7–33.3	19.6
<i>Ips amitinus</i>	1000–1099	20.8–78.1	46.7	–	–
	1100–1199	30.8–61.5	52.8	13.4–66.7	24.6
	1200	9.1–57.1	23.1	Individual data	11.1

Population density of *I. typographus* was greatest in trees growing at altitudes from 1100 to 1199 m a.s.l. (tab. 3 and 4) where there were recorded on average: 1 mother gallery/40.5 cm² and 1 exit hole/18.9 cm² of the bark. For comparison, in tree stands located at 750 m a.s.l., there were observed on average 1 mother gallery/134.2 cm² of the bark, and in trees growing at altitude at least 1200 m – 1 gallery/73.7 cm² and 1 exit hole/19.6 cm².

Fecundity: for *I. amitinus* there were found on average 20.9 laid eggs/mother gallery, and for *I. typographus* at an altitude 1000 m a.s.l. – 51 eggs/gallery.

Mortality: when determined for *I. typographus* at altitude 1000 m a.s.l. mortality was 88.5%, whereas at altitude 1200 m a.s.l. it ranged from 81.5% through 92.0% to 100% in different tree sections (tab. 4).

The analyses of small spruce bark beetle mortality under natural conditions were conducted only in 72,

73w and 163l forest compartments, and not in other sites, because there the observations were conducted on the trap trees – debarked before completion of bark beetle development. The mean number of exit holes observed was 42.25/100 cm², being close to the theoretical number of beetles developing per a unit area with no effect on mortality (the mean number of galleries amounting to 2.16 times the mean number of eggs laid in a mother gallery of 20.9 gives 45.36 beetles developing per 100 cm² area). Small spruce bark beetle mortality calculated based on the above data was 0.93%.

DISCUSSION

The small spruce bark beetle *Ips amitinus* is a typical element of bark beetle community and it accompanies the European spruce bark beetle *Ips. typographus* in spruce stands. Increasingly often, next to *Pityogenes chalcographus*, it begins to play a role of co-dominant or else dominant species, particularly in mountainous areas (Starzyk et al. 2000; Mazur et al. 2006; Plašil and Cudlín 2006; Økland and Skarpaas 2008; Witrylak 2008).

Development phenology in *I amitinus* compared to that of *I. typographus* was investigated in Finland (Annala and Nuorteva 1977). The results of the studies on spruce bark beetle biology, ecology and phenology of development carried out in Poland in the lower subalpine forests of the Beskid Sądecki Mts. were presented by Witrylak (2008).

In small spruce bark beetle feeding galleries observed in the Karkonoski National Park, the number of mother galleries ranged from 2 to 7. Almost 50% of the galleries were feeding galleries with four ones extending from the mating chamber. The number of mother galleries recorded in a single feeding gallery did not differ from the data available in literature.

I. amitinus females lay eggs in egg galleries bored on mother galleries' sides. According to Swiss data the number of laid eggs ranges from 30 to 60 (Nierhaus-Wunderwald and Forster 2004). The number of egg galleries recorded in feeding galleries of small spruce bark beetle population in the Karkonosze Mts. ranged from 9 to 48, and on average 20.92. Observed values are lower than those reported in subject literature.

I. amitinus embryogenesis typically lasts 2 weeks, while larval development takes 3 to 4 weeks. During

this period of time larvae bore larval galleries terminated with oval pupa cells and go through 3 larval stages. Pupae development lasts 2 weeks, and consequently full development of the small spruce bark beetle is completed within the period of 8 to 11 weeks. Under alpine conditions at altitude 1500 m a.s.l., development of this species lasts from the second half of May to early September (Nierhaus-Wunderwald and Forster 2004).

The comparison of the results recorded in the Karkonoski National Park with data reported in literature shows that the course and rate of development of the small spruce bark beetle in the Karkonosze Mts. are fully comparable with the results on this species population obtained under alpine conditions.

Development phenology of bark beetles, counting *I. typographus* and *I. amitinus*, depends on temperature conditions in a given season. Diurnal temperatures influence the development rate of specimens, while the so-called heat sum required for development of specimens determines the duration of development (Szudecki 1983; Plašil and Cudlín 2006 and literature sources cited therein). Particularly, spring mass emergence of bark beetle adults after hibernation, establishment of feeding galleries and the course of swarming may be prolonged as a result of low temperatures. Observations reported by Kuźmiński and Mazur (2013) indicate that the small spruce bark beetle, apart from swarming culmination that occurs in the second half of May and the turn of May and June, may colonize trees also in the later period. On many trap trees, some feeding galleries with poor (delayed) development of mother galleries was observed. This may indicate mass incidence of sister generation, which is consistent with the results presented by Witrylak (2008).

The long period of spruce colonization by small spruce bark beetles may be explained in two ways. Firstly, weather conditions may have a significant effect on the length of feeding gallery establishment period. However, this effect may pertain to the first 4 weeks, i.e. the turn of May and June. A large number of feeding galleries initiated and observed in the second half of July may indicate establishment of the sister generation (although this is not suggested by the appearance of feeding galleries, particularly the high number of mother galleries), or else establishment of feeding galleries by bark beetles overwintering in the larval stage

and pupating only in the spring. As it is indicated by observations from 2005, such trends in small spruce bark beetle population (i.e. abundance and establishment of feeding galleries throughout the season) are much stronger than those in *I. typographus*.

When comparing development phenology of the small spruce bark beetle described above with development of *I. typographus* in the Karkonosze Mts. (Mazur et al. 2006) we may their considerable similarity.

The occurrence of the second generation of *I. typographus* and *I. amitinus*, particularly under mountainous conditions of the Karkonosze, seems impossible due to the duration of development of spruce bark beetle specimens lasting until September. However, manifestation of some feeding galleries with truncated mother galleries and the small number of larval galleries observed may indicate potential emergence of sister generations. However, the number of sister generations does not seem high, since it has been reported by different authors that considerable numbers of "parental" specimens remain in feeding galleries produced by the first generation extending mother galleries.

CONCLUSIONS

- Phenology and development rate of the small spruce bark beetle in the Karkonosze Mts. are analogous with those observed in this species under alpine conditions. The mean number of laid eggs found in the Karkonosze Mts. is lower. The reproduction success of the small spruce bark beetle assessed based on the number of exit holes is very high, and consequently its mortality is very low. Yet, there should be stressed that mortality results were obtained based on the analyses of individual trees only, thus any generalization may be burdened with error.
- Colonisation of trees and establishment of feeding galleries by the small spruce bark beetle in the Karkonosze Mts. is a long process (lasting several weeks). In the second half of June new feeding galleries were established on many trees, and more than 1/3 of all feeding galleries of this bark beetle species were observed the second series traps. This indicates advisability of applying also second series of conventional trap trees in forest protection practice.

REFERENCES

- Annila E., Nuorteva M. 1977. Dates of attack and emergence of *Ips amitinus* Eichh. (Col., Scolytidae) in Finland. *Ann. Ent. Fenn.* 43 (1), 28–30.
- Biermann G., Thalenhorst W. 1977. Zur Kenntnis des kleinen Buchdruckers, *Ips amitinus* (Eichh.) (Col., Scolytidae). *Anzeiger Schädlingeskunde und Pflanzenschutz Umweltschutz*, 50 (2), 20–23.
- Brokerhoff E.G., Bain J., Kimberley J.M., Knížek M. 2006. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytidae) and relationship with establishment in New Zealand and worldwide. *Canadian Journal of Forest Research*, 36, 289–298.
- Burakowski B., Mroczkowski M., Stefańska J. 1992. Chrząszcze Coleoptera Ryjkowcowate prócz ryjkowców – Curculionoidea prócz Curculionidae (Beetles Coleoptera Spruce wood borers except for true weevils – Curculionoidea except for Curculionidae). Katalog Fauny Polski, Part 23, vol. 18, 1–234.
- Grodzki W. 1997. Changes in the occurrence of bark beetles on Norway spruce in a forest decline area in the Sudety Mountains in Poland. In: Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests (eds.: J.-C. Grégoire, A.M. Liebhold, F.M. Stephen, K.R. Day, S.M. Salom. USDA, Forest Service General Technical Report, Ne-236, 105–111.
- Grodzki W. 1998. Szkodniki wtórne świerka – kornik drukarz i kornik drukarczyk (Secondary pests of spruce – eight-toothed bark beetle and small spruce bark beetle). *Biblioteczka Leśniczego*, 95.
- Grodzki W. 2009. Entomofauna of dying young spruce *Picea abies* (L.) Karst. in the area after forest decline in the Izerskie Mountains. *Folia Forestalia Polonica, Series A Forestry*, 51 (2), 161–170.
- Holuša J., Lukášová K., Grodzki W., Kala E., Matoušek P. 2012. Is *Ips amitinus* (Coleopatra: Curculionidae) Abundant in Wide Range of Altitudes? *Acta Zoologica Bulgarica*, 64 (3), 219–228.
- Jurc M., Bojović S. 2006. Bark beetle outbreaks during the last decade with special regard to the eight-toothed bark beetle (*Ips amitinus* Eichh.) outbreak in the Alpine region of Slovenia. In: Biotic damage in forests. Proceedings of the IUFRO (WP7.03.10) Symposium held in Mátrafüred, Hungary, 12–16 September 2004 (eds.: G. Csóka, A. Hirka, A. Kotlay).
- Kicińska A., Kuźmiński R., Mazur A. 2012. Morfologia kornika drukarczyka (*Ips amitinus* Eichh.) i zmienność osobnicza populacji w Karkonoszach (Morphology of small spruce bark beetle (*Ips amitinus* Eichh.) and individual variation in the Karkonosze populations). In: Ochrona lasu – wybrane problemy historyczne i współczesne (Forest protection – selected historical and contemporary problems). Publication dedicated to Prof. dr. hab. Jacek Michalski on his birthday. Wydawnictwo Uniwersytetu Przyrodniczego w Poznaniu, Poznań, 95–120.
- Koponen M. 1975. Distribution of *Ips amitinus* Eichh. (Coleoptera, Scolytidae) in Finland in 1950–1973. *Ann. Ent. Fenn.*, 41, 65–69.
- Kuźmiński R., Mazur A. 2013. Zasiedlanie drzew przez zespół korników (Col. Curculionidae, Scolytinae) w górnoreglowych borach świerkowych w Karkonoskim Parku Narodowym (Infestation of trees by bark beetle community (Col. Curculionidae, Scolytinae) in upper subalpine spruce forests in the Karkonoski National Park). In preparation.
- Lindelöw Å. 2000. Bark- and wood-living insects in timber imported to Sweden – aspects on the risks for establishments of new species. *Aktuelt fra skogforskningen*, 4, 5–10.
- Lundberg S. 1995. Catalogus Coleopterorum Suecie. Naturhistoriska riksmuseet Stockholm.
- Mazur A., Łabędzki A., Raj A. 2006. Characteristics of forest stands in the uppermost forest boundary zone of the Karkonoski National Park. In: Insect outbreaks in managed and unmanaged forests (ed.: A. Kolk). Forest Research Institute, Warszawa, 47–58.
- Mazur A., Łabędzki A., Raj A. 2008. Obserwacje nad występowaniem kornika drukarza *Ips typographus* (L.) i gatunków towarzyszących w ekosystemach leśnych Karkonoskiego Parku Narodowego w latach 2001–2003 (Observations on occurrence of eight-toothed bark beetles *Ips typographus* (L.) and accompanying species in forest ecosystems of the Karkonoski National Park in the years 2001–2003). In: Monitoring ekosystemów leśnych w Karkonoskim Parku Narodowym (Monitoring of

- forest ecosystems in the Karkonoski National Park) (eds.: A. Mazur, A. Raj, R. Knapik). Karkonoski Park Narodowy, Jelenia Góra, 91–127.
- Nierhaus-Wunderwald D., Forster B. 2004. Zur Biologie der Buchdruckerarten. *Merkblatt für die Praxis*, 18 (3), 1–8.
- Økland B., Skarpaas O. 2008. Draft pest risk assessment report on the small spruce bark beetle, *Ips amitinus*. Commissioned report from Norwegian Forest and Landscape Institute, 10/2008.
- Plašil P., Cudlín P. 2006. Management des Borkenkäfers *Ips typographus* L. im Nationalen Naturschutzgebiet Praděd in der Tschechischen Republik. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, 15, 167–172.
- Starzyk J.R. 1987. Methods of quantitative studies on cambio- and xylophagous insects. In: IV Symposium on the protection of forest ecosystems. Wyd. SGGW-AR, Warszawa.
- Starzyk J.R., Graboń K., Hałdaś E. 2000. Cambio- and xylophagous insects in spruce (*Picea abies* (L.) Karst.) stands of the Upper San River Valley in the Bieszczady Mountains National Park (Eastern Carpathians). *Zeszyty Naukowe AR Kraków, Leśnictwo*, 29, 57–72.
- Stauffer C., Zuber M. 1998. *Ips amitinus* var. *montana* (Coleoptera, Scolytidae) is synonymous to *Ips amitinus*: a morphological, behavioural and genetic re-examination. *Biochemical Systematics and Ecology*, 26, 171–183.
- Szujecki A. 1983. Ekologia owadów leśnych. PWN, Warszawa.
- Witrylak M. 2008. Studies of the biology, ecology, phenology, and economic importance of *Ips amitinus* (Eichh.) (Col., Scolytidae) in experimental forests of Krynica (Beskid Sądecki, southern Poland). *Acta Scientiarum Polonorum Silvarum Colendarum Ratio et Industria Lignaria*, 7 (1), 75–92.